STREPTAXIDAE (MOLLUSCA, GASTROPODA: PULMONATA) FROM ALDABRA ISLAND, WESTERN INDIAN OCEAN

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INTRODUCTION

THE pulmonate gastropod family Streptaxidae has an almost circumtropical distribution. Species are particularly numerous and diverse on the African continent ; in addition the family is well represented on Madagascar, the Comoros, Seychelles and Mascarene Islands in the Western Indian Ocean. Aldabra atoll (9°24′ S 46°20′ E) is situated in the southwestern Indian Ocean (fig. 5) ; the nearest land of any magnitude is the island of Madagascar at a distance of about 420 km to the southeast and the African mainland at about 640 km to the west. Apart from very small atolls the nearest high islands are the Comoros at a distance of about 400 km to the southwest. The Seychelles are further away than both the African continent and Madagascar, viz. about 1200 km to the northeast.

Maxwell Smith (1909) was the first to record the presence of streptaxids on the island of Aldabra. Messrs J. F. Peake and J. D. Taylor have been participating in various phases of the Royal Society Expedition to Aldabra. In the course of their work on the atoll and its satellite island Assumption they have collected extensive series of streptaxid shells, the study of which they have entrusted to the present author. Aldabra and Assumption appear to harbour four species of Streptaxidae, three of which are extinct. All are described below followed by a discussion on their relationships and possible derivation.

The following abbreviations have been used :

BMNH	British Museum (Natural History), London ;
NM	Natal Museum, Pietermaritzburg ;
PSTE/JCFF	Percy Sladen Trust Expedition, leg. J. C. F. Fryer ;
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden ;
RSE	Royal Society Expedition ;
l/*d*	ratio length/major diameter of shells.

The *l*/*d* has been calculated from micrometer readings, so that these figures may not always agree with those calculated from the accompanying measurements in mm.

Acknowledgements are due to Mr J. F. Peake and Dr J. D. Taylor, and the staff of the Mollusca Section of the British Museum (Natural History) for assistance in various respects. I am also indebted to The Royal Society, who have fostered and encouraged research on Aldabra Island. Thanks are due to Dr A. Zilch of the Senckenberg-Museum, Frankfurt am Main, for hospitality for comparative studies at his institute, and to Mr R. N. Kilburn of the Natal Museum for lending the

material described by Connolly in 1925. The illustrations are due to the professional skill of H. Heijn, staff artist of the Department of Systematic Zoology of Leiden University.

Localities have been pinpointed by means of their coordinates on the Royal Society grid as shown on the map by Stoddart in Westoll & Stoddart (1971) (between pp. 632 and 633).

The fossils have been registered in the Mollusca Section, Department of Palaeontology, and recent specimens bear registration numbers of the Mollusca Section, Department of Zoology, both in the British Museum (Natural History).

Gulella gwendolinae (Preston, 1910)

Ennea gwendolinae Preston, 1910, *Ann. Mag. nat. Hist.* (8) **6** : 527, pl. 7, fig. 3 ('Shimbi Hills, British East Africa').

Gulella gwendolinae : Verdcourt, 1962, *Annls Mus. r. Afr. centr. Sér. 8° Sci. zool.* **106** : 8 ('K [= Kenya], Shimba Hills and nearby coastal forests').

Gulella gwendolinae aldabrae n. subsp.

Figs. 1, 6

Gulella gwendolinae : Connolly, 1925, *J. Conch., Lond.* **17** : 265 ('Aldabra I.') ; Germain, 1934, 67me Congr. Soc. sav. : 131 (footnote, 'Aldabra').

Ennea gwendolinae : Barnacle, 1962, *J. Seych. Soc.* **2** : 54 ('Aldabra').

Ennea alauda Sykes (nomen nudum) : Barnacle, 1962, *J. Seych. Soc.* **2** : 54 ('Ile Picard, Aldabra').

Ennea sp. : Smith, 1909, *Nautilus* **23** : 69 ('Grande Terre. Ile Picard. Iles Vertes').

Diagnosis. A subspecies of *Gulella gwendolinae* in size and shape in between the typical form and *G. g. tsadiensis* Blume, but with the aperture smaller than in the other subspecies ; dentition as in typical form, but with little variation.

Description of shell. Shell (fig. 1) small, (sub)cylindrical, with open umbilicus, smooth, creamy white. Spire produced, sides subparallel, apex flattened, obtusely conical. Whorls six to seven, slightly convex, almost completely smooth, only with faint traces of costulation or striation below the sutures and around the umbilicus, initial whorls rarely with indication of spiral sculpture ; sutures shallow, simple, somewhat impressed, (sub)crenellate. Aperture quadrate, rounded at base, peristome incrassate and reflected, white and glossy, with six-fold dentition : a reasonably well-developed oblique angular lamella touching the tip of the labrum ; two subequal mid-labral denticles on a slightly raised common base, labral complex corresponding to shallow but extensive external pit ; a mid-basal denticle, also corresponding to a little and shallow outside depression, which is sometimes hardly noticeable ; bipartite columellar process consisting of two prominent subequal denticles on a raised common base – the bifurcation of the columellar process may vary in depth.

Measurements of shell : 3·6–5·1 × 1·4–1·9 mm, l/d 2·23 – 2·84 (mean 2·53, average of 56 : 2·56), length last whorl 1·8–2·4 mm, aperture length × width 1·1–1·6 × 1·0–1·4 mm, 6–7 whorls. Table 1 details the measurements of 56 adult shells ; the holotype is no. 34.

Table 1

Measurements of shells of *Gulella gwendolinae aldabrae* n. subsp. from Aldabra and Assumption

no.	length × maj. diam.	*l/d*	length last whorl	aperture length × width	number of whorls	locality
1	3·6 × 1·4 mm	2.48	1·8 mm	1·2 × 1·1 mm	6½	Anse Cedres
2	3·6 × 1·5 mm	2·35	1·8 mm	1·1 × 1·1 mm	6	Aldabra, Sykes
3	3·6 × 1·5 mm	2·37	1·9 mm	1·2 × 1·1 mm	6	Aldabra, Sykes
4	3·6 × 1·6 mm	2·28	1·9 mm	1·2 × 1·1 mm	6	Ile Michel
5	3·7 × 1·4 mm	2·68	1·8 mm	1·2 × 1·0 mm	6½	Aldabra, Thomasset
6	3·7 × 1·4 mm	2·61	1·9 mm	1·2 × 1·1 mm	6	Anse Cedres
7	3·7 × 1·4 mm	2·60	1·9 mm	1·2 × 1·1 mm	6½	Aldabra, Sykes
8	3·7 × 1·6 mm	2·40	1·9 mm	1·2 × 1·2 mm	6	Assumption, Sykes
9	3·8 × 1·5 mm	2·54	1·9 mm	1·2 × 1·1 mm	6½	Anse Cedres
10	3·8 × 1·6 mm	2·44	1·9 mm	1·2 × 1·1 mm	6¼	Aldabra, Thomasset
11	3·8 × 1·6 mm	2·44	2·0 mm	1·2 × 1·1 mm	6	Ile Michel
12	3·8 × 1·6 mm	2·44	2·0 mm	1·2 × 1·1 mm	6½	Aldabra, Sykes
13	3·8 × 1·6 mm	2·35	2·0 mm	1·2 × 1·1 mm	6	Ile Michel
14	3·8 × 1·7 mm	2·26	2·1 mm	1·2 × 1·2 mm	6	Aldabra (a), Sykes
15	3·9 × 1·4 mm	2·69	2·0 mm	1·2 × 1·1 mm	6½	Aldabra, Sykes
16	3·9 × 1·6 mm	2·48	1·9 mm	1·2 × 1·1 mm	6½	Anse Cedres
17	3·9 × 1·6 mm	2·48	1·9 mm	1·2 × 1·1 mm	6½	Aldabra, Thomasset
18	3·9 × 1·6 mm	2·48	2·1 mm	1·3 × 1·1 mm	6	Assumption, Sykes
19	3·9 × 1·6 mm	2·35	1·9 mm	1·4 × 1·1 mm	6¼	Platin
20	3·9 × 1·7 mm	2·30	2·1 mm	1·2 × 1·2 mm	6	Aldabra (a), Sykes
21	3·9 × 1·5 mm	2·63	1·9 mm	1·2 × 1·2 mm	6	Assumption, Sykes
22	3·9 × 1·5 mm	2·63	1·9 mm	1·2 × 1·0 mm	6¾	Anse Cedres
23	3·9 × 1·6 mm	2·52	2·1 mm	1·2 × 1·2 mm	6¼	Ile Michel
24	3·9 × 1·6 mm	2·42	2·0 mm	1·2 × 1·2 mm	6¼	Ile Michel
25	3·9 × 1·6 mm	2·42	2·1 mm	1·2 × 1·2 mm	6¼	Ile Michel
26	4·0 × 1·5 mm	2·67	1·9 mm	1·1 × 1·1 mm	6¾	Aldabra, Sykes
27	4·0 × 1·6 mm	2·56	2·0 mm	1·2 × 1·2 mm	6¾	Anse Cedres
28	4·0 × 1·6 mm	2·56	2·0 mm	1·2 × 1·2 mm	6½	Aldabra, Thomasset
29	4·0 × 1·6 mm	2·46	2·0 mm	1·4 × 1·2 mm	6	Assumption, Sykes
30	4·1 × 1·5 mm	2·70	2·1 mm	1·3 × 1·2 mm	6¼	Assumption, Sykes
31	4·1 × 1·6 mm	2·60	1·9 mm	1·3 × 1·2 mm	7	Anse Cedres
32	4·1 × 1·6 mm	2·52	2·1 mm	1·2 × 1·2 mm	6¼	Ile Michel
33	4·1 × 1·5 mm	2·75	2·1 mm	1·2 × 1·1 mm	6¾	Anse Cedres
34	4·1 × 1·5 mm	2·75	2·1 mm	1·4 × 1·1 mm	7	Anse Cedres
35	4·1 × 1·6 mm	2·64	2·0 mm	1·2 × 1·1 mm	6½	Aldabra, Thomasset
36	4·1 × 1·6 mm	2·64	2·0 mm	1·2 × 1·1 mm	6¾	Aldabra, Sykes
37	4·1 × 1·6 mm	2·54	2·0 mm	1·2 × 1·2 mm	6¼	Aldabra (a), Sykes
38	4·1 × 1·7 mm	2·44	2·2 mm	1·3 × 1·2 mm	6¼	Ile Michel
39	4·2 × 1·6 mm	2·68	2·0 mm	1·3 × 1·1 mm	6½	Aldabra, Thomasset
40	4·2 × 1·6 mm	2·62	2·0 mm	1·4 × 1·2 mm	6¾	Aldabra, Thomasset
41	4·3 × 1·6 mm	2·76	2·0 mm	1·3 × 1·1 mm	7	Anse Cedres
42	4·3 × 1·9 mm	2·23	2·3 mm	1·6 × 1·4 mm	6	Aldabra (a), Sykes
43	4·4 × 1·6 mm	2·80	2·1 mm	1·4 × 1·2 mm	6¾	Assumption, Sykes
44	4·4 × 1·6 mm	2·69	2·1 mm	1·4 × 1·2 mm	7	Aldabra, Sykes
45	4·4 × 1·6 mm	2·69	2·2 mm	1·3 × 1·2 mm	6½	Aldabra (a), Sykes
46	4·4 × 1·7 mm	2·50	2·1 mm	1·4 × 1·3 mm	6½	Aldabra (a), Sykes
47	4·4 × 1·6 mm	2·84	2·2 mm	1·4 × 1·1 mm	7	Assumption, Sykes

TABLE 1 (*contd*)

no.	length × maj. diam.	*l/d*	length last whorl	aperture length × width	number of whorls	locality
48	4·4 × 1·6 mm	2·84	2·2 mm	1·4 × 1·2 mm	6¾	Assumption
49	4·6 × 1·9 mm	2·43	2·4 mm	1·6 × 1·3 mm	6½	Ile Picard, Sykes
50	4·7 × 1·7 mm	2·78	2·4 mm	1·5 × 1·4 mm	6½	Assumption
51	4·7 × 1·8 mm	2·59	2·2 mm	1·3 × 1·2 mm	7	Aldabra (a), Sykes
52	4·7 × 1·8 mm	2·59	2·2 mm	1·4 × 1·3 mm	6¾	Aldabra (a), Sykes
53	4·9 × 1·7 mm	2·82	2·2 mm	1·5 × 1·3 mm	7	Aldabra (a), Sykes
54	4·9 × 1·9 mm	2·63	2·4 mm	1·6 × 1·3 mm	7	Aldabra (a), Sykes
55	5·0 × 1·8 mm	2·76	2·4 mm	1·6 × 1·2 mm	7	Platin
56	5·1 × 1·9 mm	2·73	2·4 mm	1·5 × 1·4 mm	7	Aldabra (a), Sykes

For explanation of the localities see the text. The shells have been enumerated according to size taken from micrometer readings, which are much more accurate than their translation into mm (e.g. 62 points = 3·9 mm, but also 63 points = 3·9 mm, etc.). No. 34 is the holotype (fig. 1, BMNH); no. 49 is the 'type' of *Ennea alauda* Sykes nom. nud. Specimens nos. 5, 17, 18, and 48 show (very) faint traces of apical spiral sculpture.

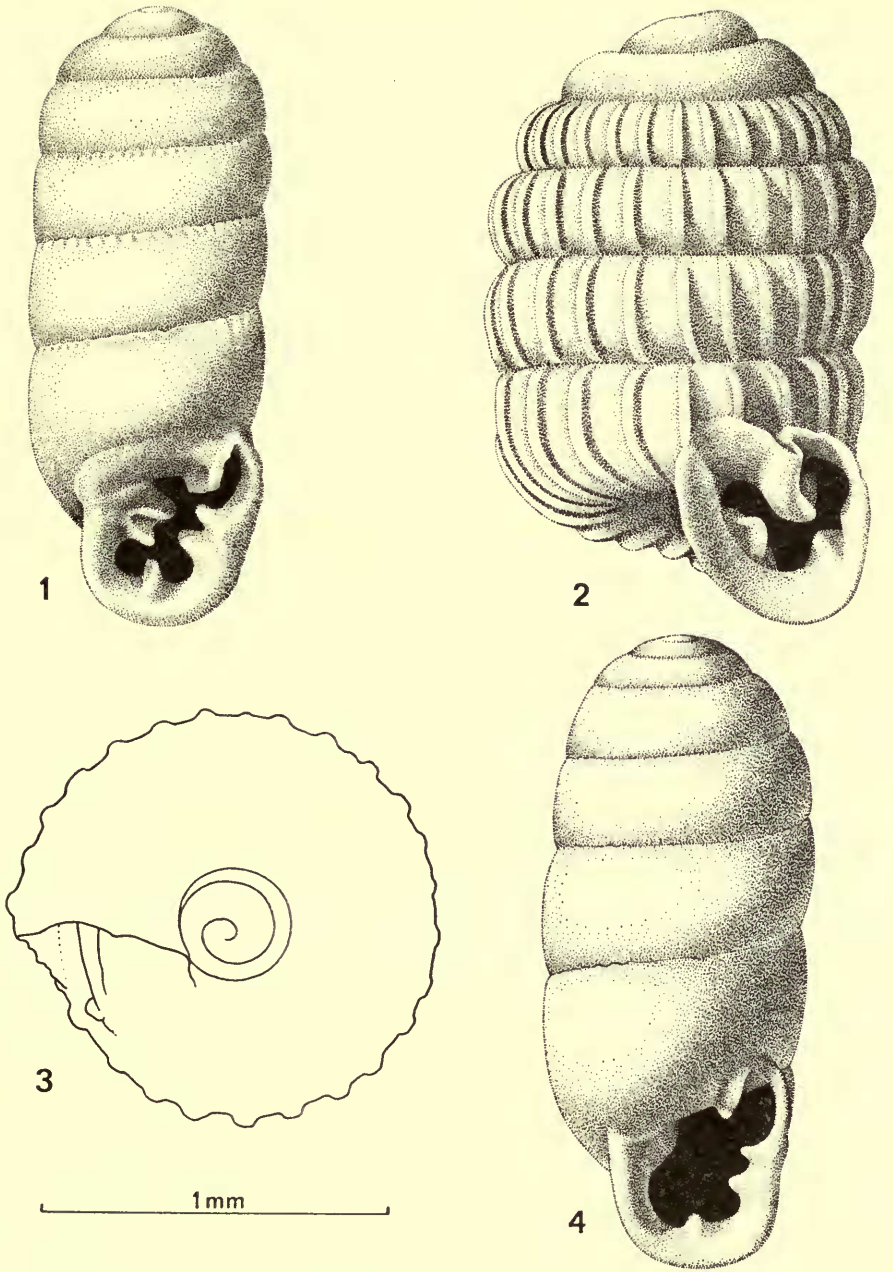
MATERIAL EXAMINED:

RECENT: Holotype, ALDABRA ISLAND: South Island (Grande Terre), Anse Cedres, c. 400 m inland (Grid ref. 359112) under stones in open grassy area amongst mature bush, 11.ix.1967, (Peake, RSE) BMNH. No. 197424. Paratypes include all material listed below, similar locality, habitat and collecting data as above, BMNH No. 197425, RMNH Nos. 54937–54939; West Island (Ile Picard), PSTE/JCFF (E. R. Sykes Colln) ['Type' of *Ennea alauda* Sykes nom. nud.], BMNH No. 197426; West Island, near village (Grid. ref. 957102), in litter around *Casuarina* trees, 7.ix.1967 (Peake, RSE), BMNH No. 197427; Ile Michel (Coconut Island, Grid ref. 325083), under stones, 14.ix.1967 (Peake, RSE) BMNH No. 197428; South Island, Platin, near pool (Grid ref. 361101), under stones, 11.ix.1967 (Peake, RSE), BMNH No. 197429; ibid, Platin, near runway trace (Grid ref. 363095), in litter amongst bush area, 9.ix.1967 (Peake, RSE), BMNH No. 197430.

Poorly localized material: ALDABRA, PSTE/JCFF, BMNH and RMNH, (E. R. Sykes Colln); ALDABRA, NM (vide Connolly, 1925: 265) (H. P. Thomasett, H. C. Burnup Colln); West Island and Takumaka (= Takamaka). N.B. two different localities, shown in Table 1 as 'Aldabra (a)', PSTE/JCFF, BMNH (E. R. Sykes Colln). ASSUMPTION ISLAND: PSTE/JCFF, BMNH and RMNH (E. R. Sykes Colln); Central area, 16.ix.1967 (Peake, RSE), BMNH No. 197433.

FOSSIL: ALDABRA ISLAND: Middle Island (Ile Malabar), Stn 31 (Grid ref. 301123), cavity fill deposit cut into Aldabra Limestone associated with *Tropidophora* sp., age less than 125 000 years BP and possibly 27 000 years BP (Taylor *et al*, RSE), BMNH No. 9921200; South Island, Stn 39D (Grid ref. 186024), Solution cavity fill cut into Takamaka Limestone buff 'soil' with abundant rootlets and associated fauna of *Tropidophora* and *Rachis*, age probably last glacial, that is post 125 000 years BP (Taylor *et al*, RSE), BMNH No. GG21201.

Note: Juvenile shells and fragments are expressly excluded from the type series. Material recorded, but not examined: ALDABRA ISLAND: Ile Verte (Smith, 1909: 69).



FIGS 1–4. Aldabra Island Streptaxidae. 1, *Gulella gwendolinae aldabrae* n. subsp., holotype shell, actual length 4·1 mm ; 2, *G. peakei* n. sp., holotype shell, actual length 2·0 mm ; 3, *G. peakei* n. sp., juvenile shell from below, to show the angular lamella in the form of a ridge extending beyond the aperture (scale applies to fig. 3 only) ; 4, *G. insulincola* n. sp., holotype shell, actual length 4·4 mm, broken in the process of drawing, but repaired. All figured specimens in British Museum (Natural History).

Distribution on Aldabra is shown in fig. 6.

There is little variation in the apertural dentition, except for the columellar complex, which may vary in the depth of bifurcation. There is no trace of apertural dentition in juvenile shells.

The above numerical data are for all material examined. The population on Assumption Island is presumably genetically separated from those on Aldabra Island proper. Assumption is situated roughly 30 km to the southeast of Aldabra. However, the number of shells available for Assumption amounts to only nine, so that no conclusions may be drawn. Measurements are in mm and the following data are shown from left to right : length × major diameter, *l/d*, length last whorl, length × width of aperture, number of specimens measured.

Aldabra : 3·6–5·1 × 1·4–1·9, 2·23–2·84, 1·8–2·4, 1·1–1·6 × 1·0–1·4, 47

Assumption : 3·7–4·7 × 1·5–1·7, 2·40–2·84, 1·9–2·4, 1·2–1·5 × 1·1–1·4, 9

Mean *l/d* 2·53, average *l/d* 2·54 (Aldabra) ; do., 2·62, 2·66 (Assumption). In both cases the shells have six to seven whorls. The range of measurements is on the whole smaller on Assumption, but this may reflect limitations imposed by the small sample.

The only local population on Aldabra which may enjoy a certain degree of spatial and consequently genetical isolation is that on Ile Michel or Coconut Island. Corresponding figures for this island also show a smaller range of measurements :

Ile Michel : 3·6–1·4 × 1·6–1·7, 2·28–2·52, 1·9–2·2, 1·2–1·3 × 1·1–1·2, 8

In this case mean and average *l/d* have values of 2·40 and 2·42 respectively and the shells have only 6–6¼ whorls. However, drawing of conclusions based on eight specimens again seems unwarranted. Ile Michel is only about 1 km from the nearest land, South Island (Grande Terre), so that there is really no question of effective isolation.

Smith (1909) recorded this species as '*Ennea* sp . . . may prove to be new'. A year later Preston (1910) described *Ennea gwendolinae* from Kenya, with which Connolly (1925) identified his Aldabra material. *Gulella gwendolinae* is known from the coastal area of Kenya (including the Shimba Hills), the Usambaras and Dar-es-Salaam in Tanzania, west of Lake Rudolf in Kenya and southeast of Lake Chad. This includes the following aberrant forms : *scissidens* Connolly, 1922 (Dar-es-Salaam) ; *porrecta* Pfeiffer, 1952 (Mombasa) ; *mkusiensis* Verdcourt, 1953 (W. Usambaras) ; *tsadiensis* Blume, 1959 (SE Lake Chad) ; var. nov. Verdcourt, 1962 (Turkana).

Notwithstanding the authority and scientific acumen of Connolly, it seems at first somewhat far-fetched to identify an Aldabra snail with a species of the African mainland. The gap between the coast of East Africa and Aldabra atoll consists of roughly 640 km of ocean, a seemingly unsurmountable barrier for a land snail. On the other hand, the character of the fauna of many islands in the western Indian Ocean is unmistakably African. The following are two quotations from Peake in Westoll & Stoddart (1971 : 581–610) : 'The affinities of the vertebrate fauna on all islands in the western Indian Ocean are predominantly orientated towards Africa' (p. 586) ; 'The fauna exhibits a wide range of affinities depending on the taxa and taxonomic levels considered ; those with Africa are dominant, . . .' (p. 606). Cogan,

Hutson & Shaffer in Westoll & Stoddart (1971 : 315–325) write : 'To summarize it may be said that the insect fauna of Aldabra is predominantly African in origin, . . .' (p. 324). Wright in Westoll & Stoddart (1971 : 299–313) concludes that the freshwater snails of the genus *Bulinus* on Aldabra are also of African origin, although some may have reached the atoll via Madagascar. All this stresses African origin and derivation, but so far no non-marine molluscan species on Aldabra has actually been identified with (East) African species. This has, however, occurred in Entomostraca (McKenzie in Westoll & Stoddart, 1971), Diptera, and Lepidoptera (Cogan, Hutson & Shaffer in Westoll & Stoddart, 1971).

The Comoros are much closer to the African continent. Although no modern summary is available, it appears from a scrutiny of a series of papers by Morelet (1860–1885) and material in various collections that African species indeed do occur here.

TABLE 2

Comparison of measurements of the shells of various populations of *Gulella gwendolinae*

material	length × maj. diam.	*l/d*	aperture length × width	number of whorls	n
aldabrae	3·6–5·1 × 1·4–1·9 mm	2·23–2·84	1·1–1·6 × 1·0–1·4 mm	6–7	56
gwendolinae	4·8–5·4 × 1·7–1·8 mm	2·82–3·09	1·6–1·8 × 1·2–1·4 mm	7	7
porrecta	5·5 × 1·9 mm	2·87	1·7 × 1·4 mm	7	1
tsadiensis	3·6–4·6 × 1·6–1·9 mm	2·00–2·50	1·7–1·9 × 1·3–1·5 mm	5½–6	29

n = number of specimens examined. Data shown under *gwendolinae* are from the holotype in the Tervuren museum, four paratypes in the British Museum (Natural History), and one paratype each in the Frankfurt and Leiden museums. Data shown under *porrecta* are from the holotype in the Frankfurt museum and those for *tsadiensis* have been extracted from Blume (1959).

In Table 2 the various forms of *G. gwendolinae* are compared ; the subspecies or varieties *scissidens*, *mkusiensis* and 'var. nov.' have not been taken into account, because these are rather aberrant. The var. *porrecta* may be a synonym of the typical form (Verdcourt, 1962 : 8). A warning may be sounded as to the number of specimens considered here. This table shows that the Aldabra form is

(a) smaller than the typical form, but larger than *tsadiensis*, although there is a wide overlap ;
(b) has a smaller major diameter than both the typical form and *tsadiensis*, although there is an almost complete overlap ;
(c) is not as slender as the typical form, but more so than *tsadiensis*, albeit with a small overlap ;
(d) has a smaller aperture than both the typical form and *tsadiensis*, with small overlaps ;
(e) has somewhat fewer whorls than the typical form, but somewhat more than *tsadiensis*.

This shows on the whole that at least three recognizable units may be distinguished, viz. the Aldabra–Assumption populations, the typical form, and the subspecies *tsadiensis*. *Gulella gwendolinae* is a variable species with an apparently wide distribution. Verdcourt (1962 : 7, footnote) rightly advises : 'Until considerable material

is available it would be as well not to bestow more names.' However, in view of the isolated location of the Aldabra–Assumption populations, it is proposed here to separate these as the subspecies *aldabrae*. Unfortunately anatomical studies are not as yet possible because of the lack of preserved soft parts.

Gulella gwendolinae aldabrae is the only recent streptaxid on Aldabra atoll. It is reasonable to expect it to have been transported from the African mainland to the island. Aldabra has always been a remote place and in view of the noticeable differences found and fossil occurrence it is unlikely that it has arrived in the wake of Man. Also, there are no records of the species from either the Comoros or Madagascar (cf. Fischer-Piette & Bedoucha, 1964b). Dispersal by tropical storms is also unlikely because of the direction of these in the area ; the animal is, however, sufficiently light to be carried by high winds. Dispersal by birds is even less likely ; the snail will certainly hardly have been picked up by the birds which now populate Aldabra. Rafting may merit consideration, but there are no suitable surface currents to effect a dispersal from Africa to Aldabra. Obviously *G. gwendolinae* has good dispersal ability, a character it shares with many small terrestrial snails (cf., e.g., Carlquist, 1965 : 292–293). For the time being no reasonably plausible explanation for the presence of *G. gwendolinae* on Aldabra is available.

Gulella peakei n. sp.

Figs. 2, 3, 7

Diagnosis. A minute species of *Gulella* with spaced lamellae and smooth interstices on the whorls, open umbilicus, and dentition consisting of angular lamella, two labral processes and columellar lamella.

Description of shell. Shell (fig. 2) small, cylindrical-ovoid, greatest width about the middle, with open umbilicus, costulate, creamy white. Spire produced, sides slightly to markedly convex, subparallel, apex somewhat flattened, obtusely conical. Whorls six to six-and-a-half, convex and sculptured with comparatively prominent, regular, straight and perpendicular, widely distant, costulae, interstices much wider than riblets, smooth, under high magnification very finely granulate. In front view the holotype shell shows only about eleven costulae on the part of the whorl above the aperture ; the last whorl has a total of about fifteen riblets. Initial two whorls smooth, very fine granulate under high magnification ; penultimate and last whorls comparatively small. Sutures shallow, simple to subcrenellate, somewhat impressed. Aperture somewhat oblique, invertedly triangular with smoothly rounded base, about as high as wide, peristome fairly thick, expanded and somewhat reflected, dentition more or less four-fold. To the right of the middle of paries a fairly large, obliquely perpendicular, angular lamella, which is nothing but a V-shaped pleat in the peristome, connected with labrum ; about half-way down the labrum a superficial swelling may be interpreted as a labral process ; somewhat below this, but much deeper inside the aperture, and at a slight distance from the tip of the angular lamella, a blunt inner labral process is seen, slightly above which there is a much smaller and less prominent process or mere swelling (not shown in

fig. 2 because hidden behind superficial labral swelling) ; columellar lamella large, blunt and prominent. The main inner labral process corresponds to a shallow depression on the outside of the aperture ; the columellar lamella corresponds to a shallow furrow on the left of the outside bottom of the aperture, thus adjoining the umbilicus.

TABLE 3

Measurements of shells of *Gulella peakei* n. sp.

no.	length × maj. diam.	*l/d*	length last whorl	aperture length × width	number of whorls	additional data
1	1·7 × 1·3 mm	1·30	0·8 mm	0·6 × 0·6 mm	6	–
2	1·8 × 1·3 mm	1·43	0·8 mm	0·6 × 0·6 mm	–	apex damaged
3	1·8 × 1·3 mm	1·36	0·8 mm	0·6 × 0·6 mm	6¼	apex damaged
4	1·8 × 1·3 mm	1·36	0·9 mm	0·6 × 0·6 mm	6	–
5	1·8 × 1·3 mm	1·39	0·8 mm	0·7 × 0·6 mm	6	–
6	1·8 × 1·3 mm	1·35	0·8 mm	0·6 × 0·6 mm	6¼	aperture rather oblique
7	1·9 × 1·3 mm	1·48	0·8 mm	0·6 × 0·7 mm	6¼	–
8	1·9 × 1·3 mm	1·48	0·8 mm	0·6 × 0·7 mm	6	–
9	1·9 × 1·3 mm	1·47	0·8 mm	0·7 × 0·6 mm	6½	–
10	1·9 × 1·3 mm	1·42	0·9 mm	0·7 × 0·6 mm	6¼	–
11	2·0 × 1·3 mm	1·57	0·9 mm	0·7 × 0·7 mm	6½	holotype, fig. 2
12	2·0 × 1·3 mm	1·51	0·8 mm	0·6 × 0·6 mm	6½	–
13	2·1 × 1·3 mm	1·55	0·9 mm	–	6½	aperture damaged
14	2·1 × 1·5 mm	1·45	0·8 mm	–	6½	aperture obscured by matrix matter

Nos. 1–13 are from Stn 34F, no. 14 from Stn 26F, Aldabra.

MEASUREMENTS OF SHELL : 1·7–2·1 × 1·3–1·5 mm, *l/d* 1·30–1·57 (mean 1·43, average of 14 : 1·44), length last whorl 0·8–0·9 mm, aperture length × width 0·6–0·7 × 0·6–0·7 mm, 6–6½ whorls. Table 3 details the measurements of 14 adult shells ; the holotype is no. 11.

MATERIAL EXAMINED :

FOSSIL : Holotype, ALDABRA ISLAND : Middle Island (Ile Malabar), Stn 34F (Grid ref. 293109), age inferred as 27 000 BP (Taylor *et al*, RSE), BMNH No. GG21202. Paratypes, similar locality and information as above, 12 shells in good condition (2–13 of Table 3) BMNH No. GG21203 and RMNH 54940–3, 14 further paratypes in poor condition or still covered by the matrix BMNH No. GG21204, numerous juvenile shells and fragments ; South Island (Grande Terre), Stn 26F (Grid ref. 337055), age uncertain but possibly same as 34F (Taylor *et al*, RSE), BMNH No. GG21205, 1 paratype (14 of Table 3) and 3 juvenile shells.

Other material : South Island, Dune d'Messe, Stn 39A (Grid ref. 186029), age inferred as 27 000 BP (Taylor *et al*, RSE), BMNH No. GG21206, some shell fragments.

Note : Juvenile shells and fragments are expressly excluded from the type series.

Distribution (fig. 7). Quaternary of Middle Island (Ile Malabar) and South Island (Grande Terre), Aldabra Island. Dr Taylor has kindly furnished the following details on the localities where *Gulella peakei* has been obtained. Stn 26F : 'Brown cavity-fill deposit in Takamaka Limestone. Many small gastropods. Age uncertain, possibly pre-125 000 yrs.' Stn 34F : 'Cavity-fill deposit cut into the Takamaka Limestone, buff 'soil' containing abundant large ribbed *Tropidophora* (only site for this species). Abundant *Assiminea, Gulella* within cavities of the *Tropidophora* and in the matrix. Almost certain last glacial, post 125 000 yrs BP.' Stn 39A : 'Solution cavity-fill cut into Takamaka Limestone. Buff 'soil' with abundant rootlets and associated fauna of *Tropidophora* and *Rachis*. Age probably last glacial, post 125 000 yrs BP.'

The species has been named after Mr J. F. Peake, Deputy Keeper of Zoology and Head of the Mollusca Section of the British Museum (Natural History), as a token of friendship and admiration for his island research.

The angular lamella is present in all juvenile shells in the form of a long and conspicuous, simple, ridge, usually stretching somewhat beyond the aperture (fig. 3). Damaged shells show that this ridge is being resorbed on the one end in the course of growth while being added to at the actual aperture. No other dental processes are present in the juvenile shells. Juvenile dentition is rare among species of the genus *Gulella* and much more common among representatives of allied genera, such as *Ptychotrema* (vide, e.g., van Bruggen, 1971, fig. 2, p. 249). Among the about 125 species of *Gulella* in Southern Africa there are about three species in which this phenomenon has been described (Burnup, 1925 ; Connolly, 1939), although juvenile shells are as yet unknown for a number of species. At least three of the species which will be considered below when trying to assess the relationships of the new species also have juvenile shells with apertural dentition, viz. *G. jacquelinae* Adam, *G. pooensis* Ortiz de Zárate & Ortiz de Zárate and *G. spatium* (Preston) (see Adam, 1965 ; Ortiz de Zárate & Ortiz de Zárate, 1956 ; Verdcourt, 1970, the latter as interpretation of Blume, 1965).

Gulella peakei has no allies on Europa Island (so far no streptaxids have been reported from this island : Fischer-Piette & Bedoucha, 1964a ; Legendre, 1966 ; Fischer-Piette & Vukadinovič, 1971), Madagascar (Fischer-Piette & Bedoucha, 1964b), the Mascarene Islands (Germain, 1921 ; Connolly, 1925), the Seychelles (Sykes, 1909 ; Connolly, 1925 ; Barnacle, 1962), the Comoros (Morelet, 1860, 1877, 1879, 1881, 1882, 1883, 1885 ; Von Martens, 1876), or Aldabra Island (Von Martens & Wiegmann, 1898 ; Smith, 1909 ; Connolly, 1925 ; Barnacle, 1962). A few of the species enumerated by Morelet for the Comoros, such as *Pupa minuscula* Morelet (1877 : 340, pl. 12, fig. 5), which may be a streptaxid, superficially resemble *Gulella peakei*, but never show the peculiar spaced lamellae on the whorls. As regards *Pupa minuscula* Morelet writes 'obsolete costulata', and 'Le test est orné de côtes fines, espacées sur le dernier tour'. *Gulella peakei* certainly does not have fine ribs, spaced on the body whorl, but rather shows widely spaced lamellae all over the shell except for the apex.

The new species obviously belongs to Verdcourt's 'Key 4' (Verdcourt, 1962 : 8). This key features East African species with spaced lamellae on the whorls. This is

probably not a natural group, although some of the species may be allied to each other. They belong to *Costigulella* Pilsbry, 1919, *Mirigulella* Pilsbry & Cockerell, 1933, and *Aenigmigulella* Pilsbry & Cockerell, 1933 ; these are all considered subgenera of *Gulella* L. Pfeiffer, 1856, by Zilch in his manual (Zilch, 1959–60 ; see also Zilch, 1961). The subgenera *Mirigulella* (monotypic) and *Aenigmigulella* (with two species, cf. Adam, 1965 : 40) are very probably products of a long and separate development ; the subgenus *Costigulella* with perhaps about ten species altogether is rather an assemblage of diverse elements. A preliminary assessment of the species of *Costigulella* shows that this subgenus may consist of three groups, viz.

(a) *G. langi* Pilsbry and *G. toticostata* Pilsbry, both from the Congo (Zaïre), and *G. pooensis* Ortiz de Zárate & Ortiz de Zárate from Fernando Poo, with lamellae and spiral sculpture on the whorls (*Costigulella* s.s.),

(b) the Kenya taxa *G. adjacens* (Preston), *G. spatium* (Preston), *G. p. pretiosa* (Preston) and *G. p. nyiroensis* (Preston), with costulae in between the lamellae on the whorls (see also Adam, 1965 : 46, who states that all three may also have costulate early whorls), and

(c) the West African species *G. hedwigae* Degner, with smooth interstices between the lamellae on the whorls.

G. microtaenia Pilsbry & Cockerell most probably does not belong to *Costigulella* s. lat. because of the 'delicate riblets' (Pilsbry & Cockerell, 1933 : 372). For the time being the present author refrains from naming the subdivisions of *Costigulella* s. lat., particularly because of the differences in dentition of the shells and the absence of anatomical data. However, zoogeographically the above three groups at first sight seem to be fairly natural : group (a) inhabits the West and Central African equatorial forest, group (b) the East African forests and group (c) the western parts of the West African equatorial forest. The subgenera *Aenigmigulella* and *Mirigulella*, both from East African forests on elevated country, may have ancestors in common with group (b). Only *Mirigulella* has a reduced dentition ; the forest element is usually of a more primitive nature than species or groups outside the forest. Therefore one may be tempted to consider all above taxa (all forest dwellers in the uplands, or lower down where the forest comes down to sea level, such as on Fernando Poo) to be more primitive than *Mirigulella*.

Compared with *G. peakei* all the above species are either too large, or have a different dentition or costulation, but usually one finds a combination of all three factors. The writer has been able to study type material or other specimens of most of these species in the museums in London, Frankfurt am Main and Leiden. *G. peakei* is not to be confused with any of the species under discussion. By virtue of the absence of sculpture on the interstices between the lamellae on the whorls the new species belongs to group (c) of *Costigulella* s. lat. Zoogeographically this is a somewhat surprising conclusion, because one hardly expects a species from Liberia and one from Aldabra to have common ancestors. Of course, the minute terrestrial snails of continental Africa are still very incompletely known and *G. hedwigae* or allied species yet to be discovered may well occur further east. Apart from other considerations it seems fairly certain that the ancestor of *G. peakei* is of continental African origin. However, the possibility that a likeness to *G. hedwigae* may have been caused

by convergent evolution cannot be ruled out. Only anatomical data are likely to help solve this question ; the fact that *G. peakei* is extinct will, however, frustrate such a project.

G. peakei is obviously extinct on Aldabra Island. Species resembling it are restricted to forest habitats in Africa ; there is no more suitable forest habitat available on Aldabra, indeed the overall impression is that of a 'semi-arid island' (Stoddart in Westoll & Stoddart, 1971 : 8). Aldabra is an elevated atoll consisting of an elevated reef situated on the summit of a mountain rising from the sea floor. There is evidence that in the past Aldabra has been much more elevated (Stoddart *et al* in Westoll & Stoddart, 1971 : 31–66, and personal communication of Dr J. D. Taylor), which must have resulted in a moister climate and consequently also the presence of a type of forest suitable for species such as *G. peakei*. Some of the islands in the Western Indian Ocean still have a fair amount of forest, but so far no apparent allies of *G. peakei* have been obtained here.

Gulella insulincola n. sp.

Figs. 4, 8

Diagnosis. A small species of *Gulella* with smooth whorls, open umbilicus, and dentition consisting of angular lamella, two labral processes, a basal denticle, and columellar lamella.

Description of shell. Shell (fig. 4) small, subcylindriform, with open umbilicus, smooth, creamy white. Spire produced, sides subparallel, apex flattened, obtusely conical. Whorls six to six-and-a-half, slightly convex, almost completely smooth, only with traces of costulation or striation behind the labrum, initial whorls smooth, very finely granulate under high magnification ; sutures shallow, simple, somewhat impressed, occasionally subcrenellate. Aperture subquadrate, rounded at base, peristome incrassate and reflected, white and probably glossy when fresh, with five-fold dentition : a reasonably well-developed slightly oblique angular lamella, touching or connected with the tip of the labrum ; two subequal mid-labral denticles on a slightly raised common base, labral complex corresponding to very shallow external pit ; a small mid-basal denticle, which usually is situated slightly to the left of the middle of the base and which may be so small as to be hardly noticeable, in which case the dentition may be interpreted as being four-fold ; columellar lamella small and little prominent, blunt and fairly deep-set.

Measurements of shell : 3·9–4·4 × 1·9–2·0 mm, *l/d* 2·07–2·29 (mean 2·18, average of 4 : 2·14), length last whorl 2·1–2·3 mm, aperture length × width, 1·3–1·6 × 1·2–1·3 mm, 6–6½ whorls. Table 4 details the measurements of four adult shells ; the holotype is no. 4.

Material examined :

Fossil : Holotype, Aldabra Island : Middle Island (Ile Malabar), Stn 34F (Grid ref. 293109), age inferred as 27 000 BP (Taylor *et al*, RSE), BMNH No. 21216. Paratypes, similar locality and information as above, 4 shells (Taylor *et al*, RSE),

BMNH No. 21217. Collected together with *Gulella peakei* n. sp. ; for details of locality see data under 'Distribution' for that species. All specimens are in poor condition, the shells being worn and very fragile.

Distribution (fig. 8). So far only known from the Quaternary of Ile Malabar or Middle Island.

TABLE 4

Measurements of shells of *Gulella insulincola* n. sp. from Stn 34F, Aldabra

no.	length × maj. diam.	*l/d*	length last whorl	aperture length × width	number of whorls	additional data
1	3·9 × 1·9 mm	2·07	2·1 mm	1·3 × 1·2 mm	6	–
2	4·1 × 1·9 mm	2·09	2·2 mm	1·4 × 1·3 mm	6+	apex damaged
3	4·2 × ±2·0 mm	±2·09	2·2 mm	1·4 × 1·3 mm	6¼	body whorl damaged
4	4·4 × 1·9 mm	2·29	2·3 mm	1·6 × 1·3 mm	6½	holotype broken but repaired

The holotype shell, no. 4, was broken, but has been repaired.

The specific name *insulincola* is a noun derived from *insula* (Lat. : island) and *incola* (Lat. : inhabitant).

The new species represents a common pattern in the genus *Gulella*. Taxa with a smooth shell and a five-fold dentition have been brought together for Southern Africa by Connolly (1939 : 20) as group 4 (ii) (10 species) and the East African ones are treated by Verdcourt (1962 : 20) in part of Key 4 (9 species). Many of these species show a dental pattern similar to that of *G. insulincola*. Among the island dwellers *G. poutrini* (Germain, 1918), which is common on Mauritius, and *G. comorensis* (von Martens, 1876) of the Comoros exhibit the same pattern. Comparison with species with the combination of characters as described above has failed to provide satisfactory identification, so that we may conclude that *G. insulincola* represents indeed a hitherto undescribed species. Its closest allies are perhaps the above species from Mauritius and the Comoros ; these differ from the new species in being much larger (sometimes twice as large), having more whorls and being less slender than *G. insulincola*. Perhaps the group with a smooth shell and a dental pattern consisting of angular lamella, two labral processes, a basal denticle, and a columellar lamella, is a natural one distributed over much of West, Central, East and Southern Africa, and on the islands in the Western Indian Ocean as well. The possibility that *G. poutrini* and *G. comorensis* may be the components of a superspecies or represent the subspecies of a widely-dispersed species may be merely food for thought in this respect. On the other hand, a shell type such as has been discussed here occurs throughout the genus *Gulella* and may well be the result of convergent evolution.

G. insulincola is obviously extinct on Aldabra, which may also be due to the fact that suitable habitat has disappeared in the course of the process of the island becoming progressively drier.

Gulella spec.

There are two specimens (BMNH) which represent a fourth species of the genus *Gulella*. Both are clearly fossils. The one, from 'Stn 34F' (see sub *G. peakei* sp. n.), is a juvenile shell of 3·2 × 2·0 mm with five whorls, of which the initial ones are smooth and the others sculptured with somewhat undulating costulae. The other

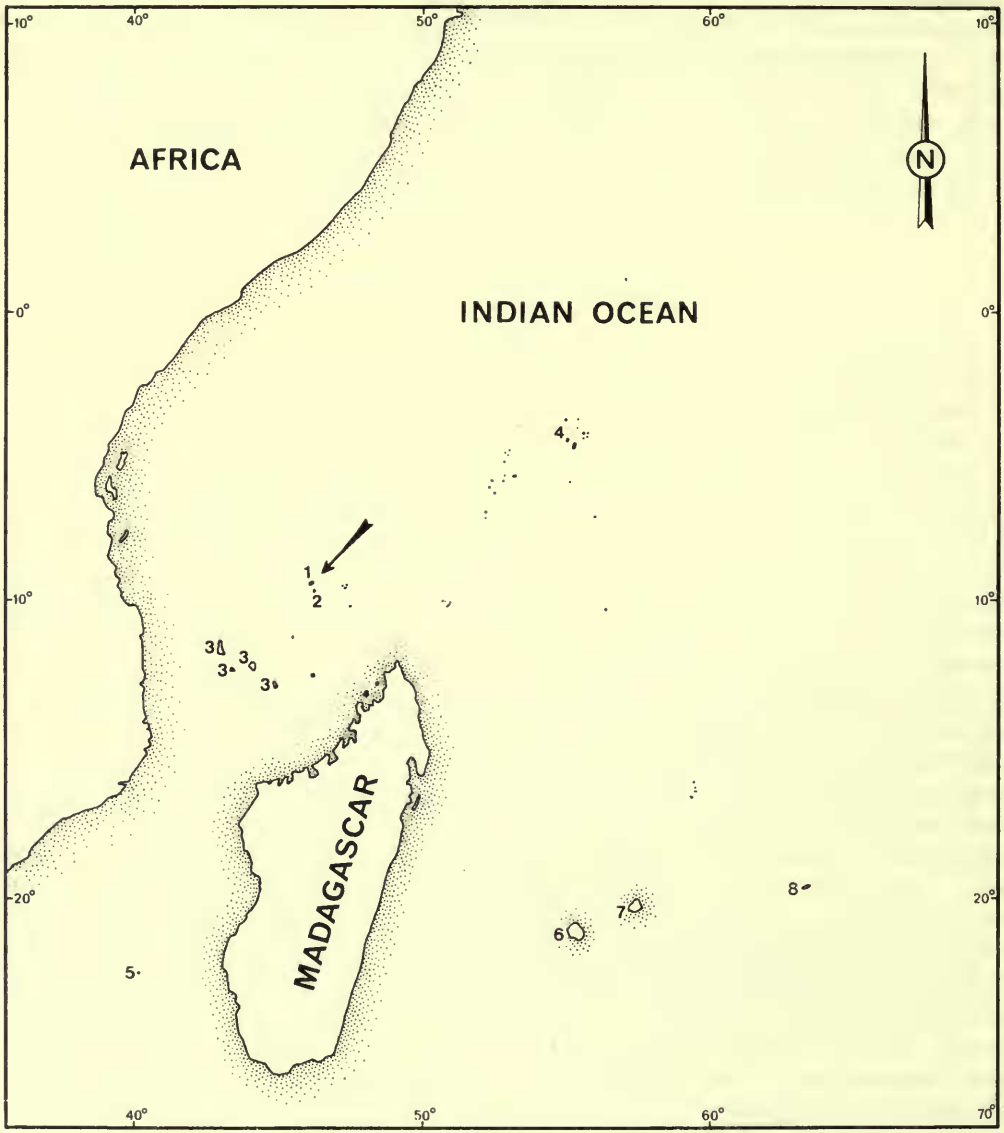


FIG. 5. Map showing position of Aldabra Island. 1, Aldabra; 2, Assumption; 3, Comoros; 4, Seychelles; 5, Europa; 6, Reunion; 7, Mauritius; 8, Rodriguez (6–8 Mascarenes).

specimen is a much younger juvenile shell of probably the same species ; it measures only 2·3 mm and the aperture is filled with matrix matter. This shell was obtained not far from the settlement on West Island (Ile Picard), grid ref. 063 E–098 N (fig. 8), 'cavity-fill cut into Basin Cabris calcarenites and Takamaka limestone, 'white soil' also containing *Rachis* and *Tropidophora*. Age uncertain ; could be the same as 39A and D'. (Notes supplied by Peake and Taylor ; Stns 39A and 39D have been described above under the other species.) No opinion as regards identity of the present species is ventured here : it is most likely that this is also an extinct species.

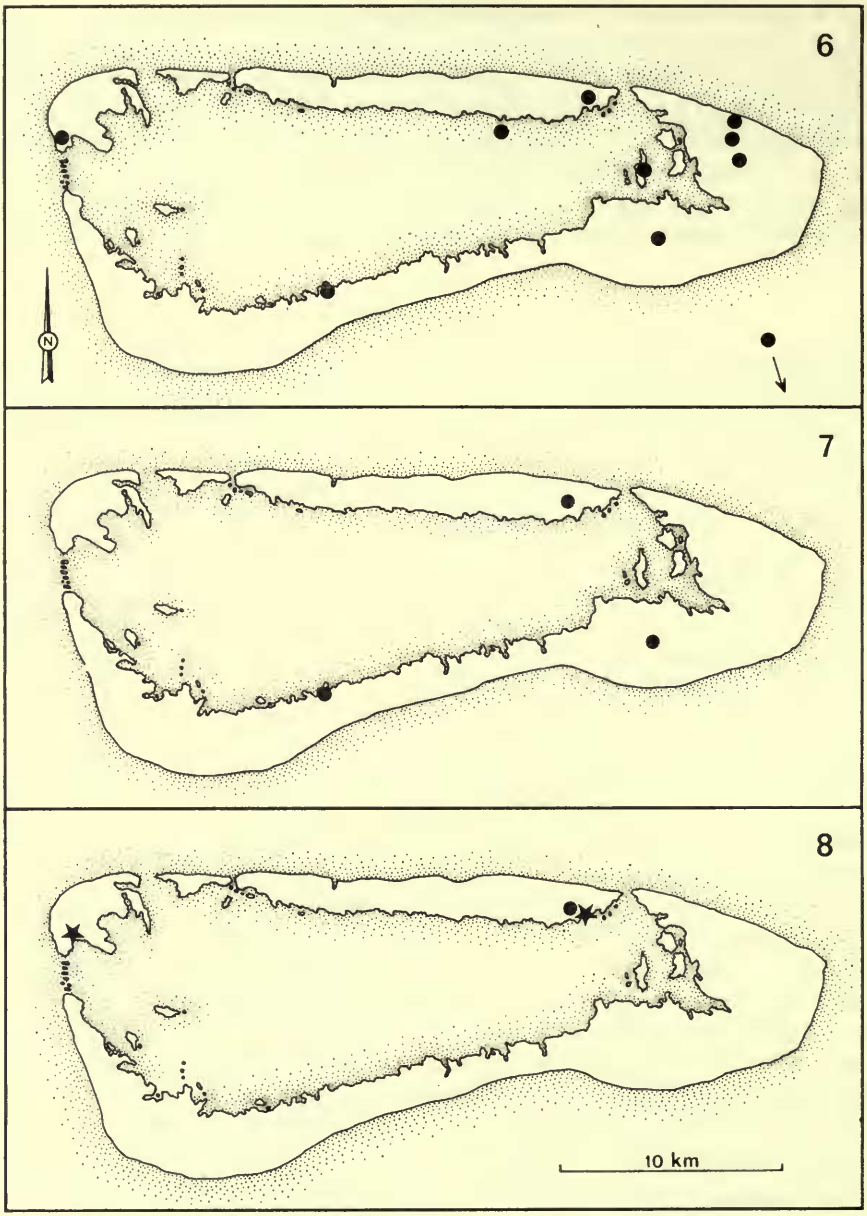
DISCUSSION

A thorough survey of the terrestrial molluscs of Aldabra has revealed the presence of four species of Streptaxidae, viz. *Gulella gwendolinae aldabrae* n. subsp., the only Recent representative of the family on the island, and three extinct taxa, *G. peakei* n. sp., *G. insulincola* n. sp. and an incompletely known species, *G.* spec.

The family Streptaxidae has excellent dispersal abilities, at least in the Western Indian Ocean. Streptaxids have reached both the Seychelles and the Mascarene Islands at distances of 1400 and 2500 km from the African mainland respectively. The Mascarene Islands are also situated betweeen 700 and 1300 km from Madagascar from whence some streptaxid ancestors may have been derived (fig. 5). Asia (India) is more than 2500 km from the Seychelles and there are few direct relationships (if any) with the streptaxids of that continent.

G. gwendolinae is a very widely dispersed African species with a tendency to become locally separated into reasonably recognizable subspecies. Its dispersal abilities are sufficiently illustrated by its wide distribution on Aldabra and Assumption (fig. 6) ; moreover, it is also locally abundant – sufficient reason to consider it a successful species in an evolutionary sense. Perhaps the adaptability to widely divergent climatic conditions and types of vegetation has been the key to its success in Africa, which at the same time has accounted for its continued survival on Aldabra. Fossil occurrence shows that it has been on the atoll for a long time, very probably having been already a contemporary of the extinct *G. peakei*, *G. insulincola* and *G.* spec. Streptaxids are carnivores known to feed on soft invertebrates, mainly other terrestrial molluscs, and particularly snails of the pulmonate family Subulinidae (van Bruggen, 1967 : 186), which family is not (yet?) known to occur on Aldabra. However, there are Subulinidae on the high islands of the Western Indian Ocean. There are a few other land snails on the atoll, of which the enid *Buliminus* (*Rhachis*) *aldabrae* von Martens, 1898, is 'The most common of all the species from Aldabra.' (Smith, 1909 : 70 ; see also Connolly, 1925 : 264–266). Fossil evidence indicates that many terrestrial snails were contemporaries of *G. peakei*, *G. insulincola* and *G.* spec.

G. peakei, *G. insulincola*, and *G.* spec. are extinct and may well have been inhabitants of types of vegetation which have disappeared on Aldabra. The relatives of at least *G. peakei* are restricted to forest habitats such as are no longer available on Aldabra. There are still remnants of forest on high islands, e.g. the Comoros, Seychelles and Mascarene Islands, of which the latter two have species of *Gulella*



FIGS 6–8. Maps showing the distribution on Aldabra Island of 6, *Gulella gwendolinae aldabrae* n. subsp. (the arrow points to Assumption) ; 7, *G. peakei* n. sp. ; 8, *G. insulincola* n. sp. (dot) and *G.* spec. (asterisks).

which may be the nearest allies of *G. insulincola*. This species or its ancestors may therefore have arrived secondarily from these islands, although Aldabra is closer to the African continent than both the Seychelles or the Mascarene Islands. There is

also other evidence that Aldabra once harboured a much more varied flora with forest components and that a progressive drying out of conditions has caused these to disappear together with the forest dwellers among the animals that led a sheltered life in the then available leaf mould. This has caused some of the predators, the three *Gulella* species, and perhaps also their prey, species of the family Subulinidae, to disappear for ever.

Finally one has to consider how the streptaxids have reached remote Aldabra. The island has never been connected with the African continent, but Aldabra streptaxids have strong links with those from that continent. Dispersal through human agency, by tropical storms, by birds, and by rafting have all been ruled out when *G. gwendolinae aldabrae* was discussed above. The same applies, *mutatis mutandis*, for the extinct species. Yet, much of the present flora and fauna of Aldabra atoll or their ancestors have obviously come from Africa. Perhaps dispersal along the usual paths has taken place in the past when the direction of wind and surface currents was more favourable to such a process than today.

The present article was finalized early in 1973. Therefore the following comprehensive paper on the land molluscs of the Comoros has not been taken into account : Fischer-Piette, E. & Vukadinovic, D. 1974. Les mollusques terrestres des Iles Comores. *Mem. Mus. natn. Hist. nat. Paris* (N.S.) (A) **84** : 1–76. The checklist includes various African species. The family Streptaxidae appears to occupy a dominant position with 46 species. *Gulella gwendolinae aldabrae* n. subsp. should be compared to *G. dentiens* (Morelet, 1883) as figured by Fischer-Piette & Vukadinovic (fig. 18 on p. 59).

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